

Neodarwinism and Macroevolution

Arguments on Evolution: A Palaeontologist's Perspective

by Anton Hoffman, Oxford University Press, 1989, £22.50/hard £10 + 27p paperback ISBN 0 19 504432 5

In this book, Hoffm—on inventively tries to convince readers that the generalised theory of evolutionary forces within populations—adequately accounts for the history of the biogeograph (p. 17). That is, some of the dark and broody are not subject to any processes and thus additional to neodarwinism. Therefore, studies of long-term patterns (as in palaeontology) are deemed to remain idiosyncratic, describing unique events, rather than deterministic or law-generating ('could' claimed the opposite).

Hoffman keeps his opening promise that his book is one of unshamed advocacy of these claims. In some early black-and-white gangster films, the 'good guys' wore white hats and the villains (black ones) from stars to bikers, so that viewers were spared confusion as the numerous protagonists headed their way through—the plot. A similar relentless dichotomy pervades this book: all who defend neodarwinism adequately, albeit for conflicting reasons, wear white hats throughout. The black-hatted crowd are united by proposals of various (mostly different) expansions or revisions of neodarwinism. (Some are criticised in the preface. 'The ideas advocated by Miles McKinney, Stephen Jay Gould, David Rouse, Jack Sepkoski, Steven Stanley, and Elisabeth Vrba are the prime targets of my criticism in this book'.)

Many of Hoffman's sweeping claims are not well supported by evidence or reasoning. One of his basic assertions is that there can be no ordering of 'incidents' or 'work' among macro-processes; for instance, that (p. 206) 'every mass extinction ... appears to be unique, both in its causes and in its effects', and that trends in spite of phylogenetic constraint cannot be consistent rules of process. All are chaotic clusters of causally independent microevolutionary events, the unique products of 'historical contingency'—and 'essentially joint action of a variety of factors'. In order to maintain his position, Hoffman dismisses the persistence of any heritable regular characters. He makes clear that he sees even aggregated (summed organisms) characters that vary regularly between lineages of species, as 'incoherent and as threatening to his overall view, for example on p. 144: 'species extinction can in principle present a serious challenge to the neodarwinian paradigm because it is

supposed to act upon entities ... each having a number of features that vary among but are invariant within species and that can be transmitted in the process of speciation to all daughter species'.

Abundant evidence contradicts these arguments. How could phylogenetic analysis succeed if there were no features that vary among but are invariant within species and that can be transmitted in speciation? If we discard the notion that some organismal features distinguish species, and that hierarchically nested sets of phenotypes have characterized each one of progressively more inclusive clades (or longer and longer eras), we also discard the best evidence that extinction has occurred. There is also cladistic evidence that even emergent species characters (e.g. population size, breeding composition, variation patterns) can be fairly characteristic species and clades over long periods.

Many long-term patterns remain unexplained precisely because their amazing regularity—across very different kinds of organisms and ecologies—does not follow idiosyncratically from traditional theory. Some of these cry out for analyses in terms of lineage-specific characters that influence characteristic evolutionary responses (such as, alleles for some characters that are closely similar within but differ between large clades) and the role of positive correlation between speciation and extinction rates across groups from protozoans to vertebrates). Furthermore, numerous recent analyses have found evidence that the controls of speciation rates, trends and phylogeny-specific responses to mass extinctions episodes involve heritable characters of lineages, and can show consistent patterns across different phylogenies (see review in Ref. 2). Such analyses posit parallelism and convergence among subsets of neodarwinian processes as having systematically repeated importance in macroevolution. Therefore, they propose theory additional to neodarwinism, because the theory of a combination of processes (including why those particular combinations should exist or be repeated, with others are absent or less frequent) is not the same as the sum of the separate theories.

In criticizing Ruse and Sepkoski's proposal of periodic mass extinctions, Hoffman extends his diatribe for regular and repetitive long-term causal processes beyond the biological, and on to global physical changes. 'They too must be chaotic clusters of multiple causally independ-

ent "mass-events", in his view, I was puzzled by this because there is at least a proposal for regularity in a biotic macro-pattern that does not involve (necessarily) biotic forces—a proposal that Ippolito, who is best on explaining such forces, off the book, I was further puzzled because so many regular biotic phenomena over shorter time-scales derive directly from longer physical periodicities (like seasons, and the Milankovitch climatic cycles occur about every 20 000, 40 000 and 100 000 years). I would have thought that our old hypothesis might be that we would discover periodic physical influences on evolution over longer and longer time scales, as the geological record improves. It seems that Hoffman denies paleontologists any role in discovering processes with long time constants—physical or biotic. (The error of such denial lies at the heart of the denunciations. For instance, the far-sightedness fossil record led to the currency of the Milankovitch cycles.) Hoffman argues (p. 206) that, even if mass extinctions occurred periodically, 'it could not pass by and any profound change in evolutionary biology'. I find the 'taking out of this possibility simply wrong. As argued by others, the small samples of survivors of regular mass extinctions will not necessarily be the fittest in the darwinian sense. Whether such samples are found to be random or consistently biased by similar causes, popular new traits in our causal concepts of life's diversity are likely to result.

I enjoyed our differences of opinion. They reflect the diverse explorations in macroevolutionary biology that make this such an unusually exciting field. To read a book of a strong and single-minded orientation that differs fundamentally from one's own also offers the opportunity to gain an overview from the other side of the fence', provided the one whose remains informed, broad and full in its coverage. In these respects I was at times disappointed in this book.

Some issues that are central to the debates addressed by Hoffman seem to have passed him by. For instance, the hierarchical levels of organisational complexity among and within living things (with the accompanying distinction between their aggregate and emergent properties), and the role of these phenomena in evolutionary theory, hardly feature in this book. He spends pages on arguing that species sorting determined by organismal selection is not species selection. This has been argued for many years, although the relevant texts are not a hind for Hoffman. But

Arguments On Evolution A Paleontologists Perspective

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